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RESPONSES OF SPINOCERVICAL TRACT NEURONES TO NOXIOUS STIMULATION OF THE SKIN

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SUMMARY

1. Activity of single spinocervical tract neurones has been recorded in the lumbar spinal cord of chloralose anaesthetized or decerebrated cats. Reversible spinalization was produced by cold block at L3. Sensitivity of these neurones to noxious stimulation was studied by heating their cutaneous receptive fields above 40–45° C.

2. Most of the units were located in lamina IV of the dorsal horn and had their receptive fields in the ipsilateral foot. All but one of the studied neurones were excited by moving hairs or by gentle mechanical stimulation of the skin.

3. Eighty-four % of the units were affected by noxious stimuli and three kinds of response were obtained: (i) 61 % were excited (E-cells) by noxious heat; (ii) 19 % were inhibited (I-cells); and (iii) 19 % gave a mixed response reversing from excitatory to inhibitory (EI-cells).

4. E-cells had axons with a wider range of conduction velocities than the rest and also received the strongest descending inhibition from supraspinal structures.

5. The recording sites of EI-cells were located in the medial third of the dorsal horn whereas E- and I-cells were distributed over the full width of the dorsal horn.

6. The possible role of the spinocervical tract in nociception is discussed.

INTRODUCTION

The spinocervical tract is one of the major ascending somatosensory pathways in the spinal cord of the cat, its anatomical presence and functional relevance in other mammals have, however, been questioned (for a detailed review see Brown, 1973). In the cat the spinocervical tract arises from

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cells in the dorsal horn (Bryan, Trevino, Coulter & Willis, 1973; Brown, House, Rose & Snow, 1976) and projects to the lateral cervical nucleus via the ipsilateral dorso-lateral funiculus (Morin, 1955; Lundberg & Oscarsson, 1961; Taub & Bishop, 1965). According to carefully controlled experiments the main source of excitatory inputs to the spinocervical tract cells arises from receptors located in the hair follicles; however a proportion of spinocervical tract neurones can be fired in addition by strong pressure, pinch, heat above about 45° C and by intense cold below about 20° C (Brown & Franz, 1969). These stimuli are known to excite nociceptors in the skin (Iggo, 1959; Burgess & Perl, 1967, 1973; Iggo & Young, 1975) and it can thus be concluded that a proportion of spinocervical tract neurones receives excitatory inputs from both sensitive hair follicle mechanoreceptors and nociceptors. Using electrical stimulation of peripheral nerve fibres, Brown, Hamann & Martin (1975) reported that almost 70% of the spinocervical tract neurones receive a mixed excitatory input from both A and C cutaneous afferent fibres and that C fibres either excite spinocervical tract neurones or have no effect on transmission through the spinocervical tract.

The pathway for the conduction of nociceptive information to the brain has, however, been classically attributed to the crossed spinothalamic tract (for review see Kerr, 1975), (the 'Vorderseitenstrange' (anterior tract) of Edinger, 1889), which is present in practically all the vertebrates (Neiuwenhuys, 1964) including the cat (Trevino, Maunz, Bryan & Willis, 1972; Trevino & Carstens, 1975). A comprehensive account of the responses of spinothalamic tract neurones to natural cutaneous stimulation is not available for the cat, but it is already known that many Waldeyer's marginal cells (Waldeyer, 1889) in the lumbar spinal cord of the cat are selectively excited by nociceptors (Christensen & Perl, 1970; Cervero, Iggo & Ogawa, 1976*b*) and project to the thalamus (Trevino & Carstens, 1975), via the crossed ventro-lateral quadrant (Kumazawa, Perl, Burgess & Whitehorn, 1975). These results support the idea of direct involvement of the spinothalamic tract in nociceptive mechanisms in the cat. The existence of this pathway as well as other possible nociceptive mechanisms such as the 'dorsal column post-synaptic system' (Angaut-Petit, 1975*a*,*b*), and the presence of a great deal of dorsal horn neurones excited by nociceptors (Wall, 1960, 1964), makes systematic study of the extent and functional relevance of the spinocervical tract in nociception necessary.

In the present paper we report an investigation on the responses of the spinocervical tract neurones to noxious stimuli applied to the skin. Identified spinocervical tract neurones have been recorded in the lumbar spinal cord of the cat and their responses to noxious stimuli were tested by

heating the skin with radiant heat. The strong descending inhibitory influences that alter the responsiveness of dorsal horn neurones and flexor reflexes to noxious stimuli (Eccles & Lundberg, 1959; Wall, 1967; Brown & Franz, 1969; Brown, 1971; Brown, Kirk & Martin, 1973; Handwerker, Iggo & Zimmermann, 1975) have been examined using a reversible spinalization technique. A preliminary report has been published (Cervero, Iggo & Molony, 1976*a*).

METHODS

Thirteen cats weighing 1·5–3·3 kg have been employed. Four cats were decerebrated at mid-collicular level under halothane anaesthesia which was discontinued thereafter and nine were anaesthetized with chloralose (60 mg.kg^{-1}), after induction with nitrous oxide/oxygen/halothane, plus additional doses of chloralose when necessary. The femoral blood pressure was recorded continuously and the diastolic pressure was maintained above 80 mmHg. The trachea was cannulated and end-tidal CO_2 maintained at 3·5–4·5%. Injections of 1·5–2 ml. 1 M sodium bicarbonate were administered every 4 hr after the beginning of each experiment to compensate for changes in blood pH which are not always reflected in the end-tidal CO_2 (D. S. McQueen, personal communication). Rectal temperature was monitored by means of a thermistor probe and maintained at 37–38° C by feed-back control of a heating blanket. On completion of the surgical preparation the animal was mounted in a frame (Clark & Ramsey, 1975), paralysed with gallamine triethiodide and artificially ventilated with room air. Two laminectomies were performed; one in the upper cervical and one in the lower lumbar regions. Pools made with skin flaps were filled with warm liquid paraffin (B.P.). Lumbosacral cord temperature was maintained at 38·5° C by feed-back control of heating coils immersed in the pool. A metal thermode was placed on the dorsal surface of the L3 segment of the cord to allow reversible cold spinalization of the cat (details of this technique have been published, Cervero *et al.* 1976*b*). Both hind limbs were shaved and both feet fastened to wooden platforms attached to the animal frame.

Electrophysiological recording and stimulating techniques. Extracellular and occasionally intracellular recordings of spinocervical tract neurones were made at the L7 segment of the spinal cord using glass micro-electrodes filled with 4% pontamine sky blue in 0·5 M sodium acetate. The most rostral L7 rootlet was mounted on Ag/AgCl electrodes to permit electrical stimulation of the afferent fibres and another pair of electrodes was placed centrally on the same rootlet to record compound action potentials evoked by the former stimulation. The spinal cord entry of this rootlet was used as a landmark in an attempt to standardize the recording locations from different animals. Distances between electrodes and between them and the micro-electrode were measured. The latency of the response of each spinocervical tract neurone to electrical stimulation of the rootlet was measured. This provided an estimate of the monosynaptic connectivity of afferents to the spinocervical tract neurones. Recordings were made on magnetic tape and 'on-line' and 'off-line' analysis of data was carried out using a PDP-12 computer.

Natural stimulation of the skin. Mechanical stimuli were either innocuous, such as brushing the skin surface or the hairs or applying steady light pressure with von Frey's calibrated hairs, or noxious squeezing of the skin with smooth and serrated-tip forceps. The thermal noxious stimulation was provided by a quartz-halogen lamp focused on the skin and controlled to raise the skin temperature up to 60° C. The

temperature of the skin surface was continuously monitored with a calibrated thermistor bead.

Identification of the spinocervical tract cells. The technique for identification of spinocervical tract cells was similar to that described by Brown & Franz (1969). After sectioning the dorsal columns at C5 level, pairs of silver electrodes were placed on the ipsilateral dorsolateral funiculus at C1 and C3 spinal cord segments. As the recording micro-electrode was lowered into the lumbar cord, electrical stimuli were delivered to the dorsolateral funiculus at C3 until an antidromic action potential was recorded. Evidence that the action potential was being conducted antidromically was confirmed by the registration of a response at a constant latency from the stimulus and by the ability of the unit to follow a train of stimuli at 300 Hz or more. Units were assigned to the spinocervical tract if there was no antidromic response from C1, if the conduction velocity of the axon between C1 and C3 was 50% or less than the velocity between C3 and the recording site, or if the threshold for antidromic excitation of the unit from C1 was ten times or more than the threshold to excite the unit from C3. Collisions between the antidromic spike and orthodromic action potentials evoked by natural stimulation of the receptive field of each neurone were considered as further evidence that the orthodromic discharges observed belonged to the spinocervical tract unit being tested.

Histological methods. The recording micro-electrode was inserted on a grid with a spacing of 200–250 μm between the parallel tracks in the L7 segment of each cat, starting at the dorsal rootlet entry of the stimulated dorsal rootlet. Superficial blood vessels were avoided. The depth of each spinocervical tract unit from the surface of the spinal cord was measured using the micromanipulator and at the end of the experiment a scale was made in the last track by electrophoretic deposition of pontamine sky blue (Hellon, 1971) at 2000 and 1000 μm. The spinal cord was removed, frozen immediately and the locations of the marked spots established from 40 μm frozen sections counterstained with hematoxylin-eosin. The locations of the recorded spinocervical tract units were calculated according to the grid made during the experiment using the marked spots as a scale. This system helps to eliminate errors which occur when locating units on the basis of micromanipulator meter readings alone.

RESULTS

Location and conduction velocities of spinocervical tract neurones

Results obtained from sixty units are presented in this paper. The locations of the recording sites of fifty-seven of these units were obtained and have been superimposed on a 'standard' transverse section of the L7 segment of the spinal cord (Fig. 1*A*) in which the laminae of Rexed (1954) are indicated. Thirty-seven (65%) of the recording sites were located in lamina IV, nine (16%) in laminae I–III and eleven (19%) in laminae V–VI.

The conduction velocities of the axons of the SCT neurones were calculated from the latencies of the antidromic spikes and the measured conduction distances. The conduction velocities ranged between 12 and 92 m/sec, with a mean of 45·18 m/sec (Fig. 1*B*).

Receptive fields

Peripheral receptive fields were determined for fifty-one neurones. Of these, fifty were excited by hair movement or light stroking of the skin. No attempt was made to determine which particular kinds of hair were effectively being stimulated. No units were found which were excited by light mechanical stimulation of the foot-pads.

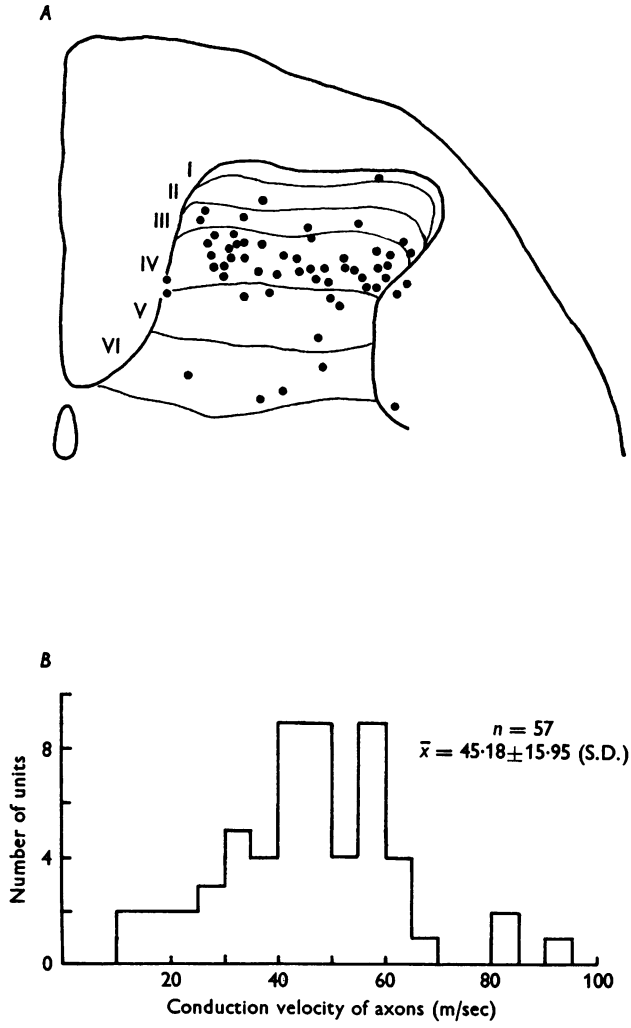

Fig. 1. *A*, location of fifty-seven spinocervical tract neurones obtained by superimposition of recording sites on a transverse section of the L7 segment of the spinal cord. Lamination according to Rexed (1954). *B*, histogram of the conduction velocities of spinocervical tract axons. The mean and S.D. of the observation are shown.

It was not possible to find a receptive field in the anaesthetized state of the preparation for the remaining unit but after blocking the spinal cord a well-defined receptive field was found from which the neurone could be excited by pinching or squeezing the skin or by heating the skin above 45° C.

All our recordings were made within a small area of the L7 and 6 segments of the spinal cord. From the entry point of the most rostral L7 dorsal rootlet, recordings were made covering the whole width of the dorsal horn and rostrally for up to a maximum distance of 2 mm (Fig. 2). Most of the receptive fields were located in or around the toes, or in the distal part of the limb, either on the ventral or dorsal aspects. Exceptions were a few units located in the lateral part of the dorsal horn whose receptive fields were on the thigh (Fig. 2). No bilateral or contralateral excitatory receptive fields were found.

Responses of spinocervical tract neurones to electrical stimulation of the afferent fibres

Fifty-two neurones were tested by electrical stimulation of the L7 dorsal rootlet. Of these twelve were not excited and eight of them have been indicated with circles in Fig. 2. They were intermingled in the dorsal horn with others which were excited by electrical stimulation of the rootlet and their receptive fields were similar to those of the rest of the sample. The forty units responding to electrical stimulation had thresholds corresponding to excitation of group II afferent fibres. Twenty of them also showed a late discharge when the intensity of stimulation reached the threshold for C-fibres as indicated by the appearance of the C-fibre wave in the compound action potential recorded from the dorsal rootlet.

Only seven units showed latencies to electrical stimulation (> 3 msec) of the dorsal rootlet outside the estimate for a monosynaptic connexion. These units (encircled with dashed lines in Fig. 2) were either in the most lateral part of the dorsal horn or medially in a zone distant from the entry point of the stimulated rootlet. Units with suspected monosynaptic connexions were, however, also found close to these regions.

Background activity

All the neurones studied showed spontaneous activity in the spinalized state of the preparation and thirty-eight (81 %) showed background activity in the anaesthetized or decerebrated states. The mean frequency of this spontaneous activity varied between units and was dependent upon the type of preparation (see below). Spontaneous activity usually consisted of occasional spikes and high frequency bursts with irregular presentation and was enhanced after noxious stimulation of the receptive

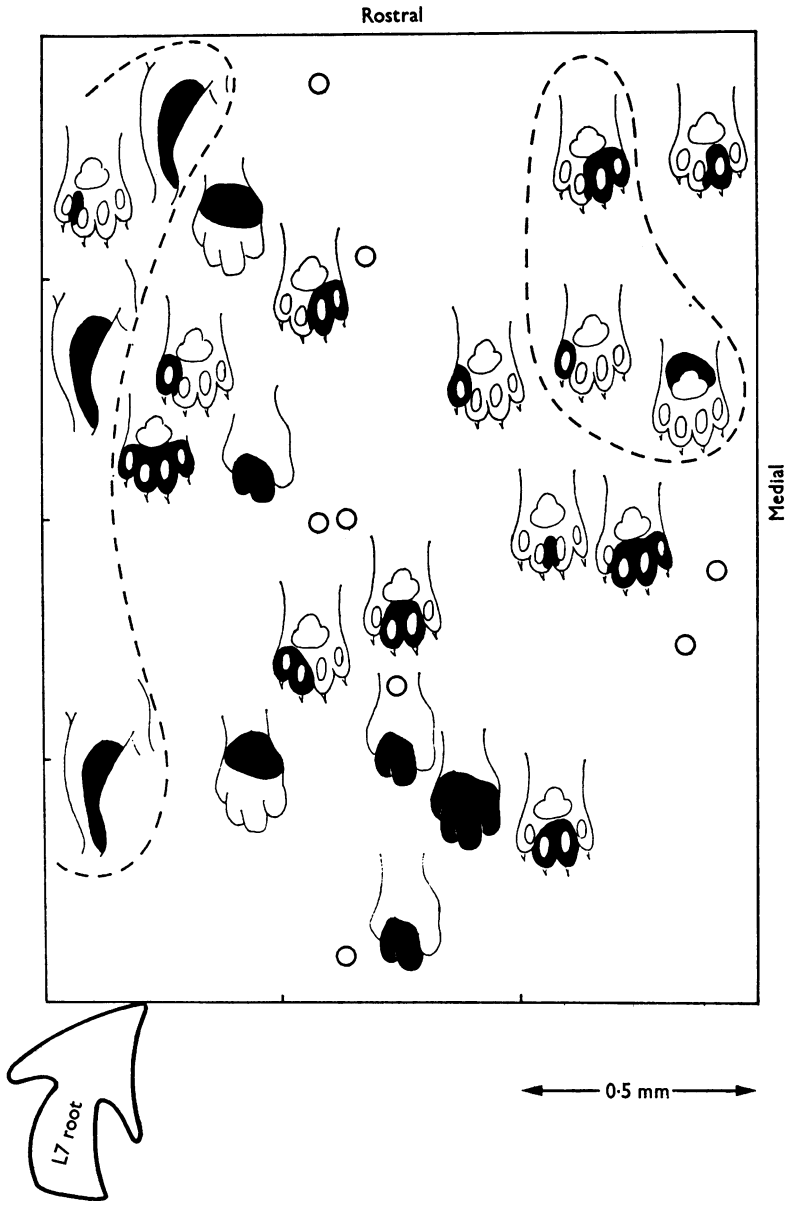

Fig. 2. A schematic plan view of parts of the left L7, 6 segments of the spinal cord with outline drawings superimposed to show the location of units and their receptive fields. Those enclosed by dashed lines were driven polysynaptically by electrical stimulation of the most rostral L7 dorsal rootlet (indicated by the large arrow in the bottom left corner) while the others were driven monosynaptically. Small circles indicate the location of units not driven by electrical stimulation of this dorsal rootlet. These units had receptive fields which were similar to units nearby. Data have been pooled from several experiments.

field or after repetitive electrical excitation of the non-myelinated afferent fibres.

Responses of spinocervical tract neurones to noxious stimuli

Thirty-seven units were tested thoroughly enough to be classified. Tests included both non-noxious and noxious stimulation. These were applied to the centre of the receptive field from which the neurone could be excited by moving hairs (its excitatory receptive field). No studies were made of ipsilateral or contralateral inhibitory receptive fields. The following responses were distinguished.

Neurones activated only by light mechanical stimuli

Five neurones (13·5 %) responded only to hair movement or to gentle stroking of hairy skin. No responses were obtained by squeezing or pinching the skin and no excitatory responses were obtained by heating the skin above 45° C.

Neurones activated only by noxious stimuli

Only one neurone belonged to this group. As described above no receptive field could be found for this unit in the anaesthetized state of the preparation but, after blocking the spinal cord at L3, a receptive field was found from which the neurone could be excited by pinching, squeezing or by heating the skin above 45° C. When the spinal cord block was removed the neurone returned to its previously unresponsive state.

Neurones activated by light mechanical stimulation and affected by noxious stimuli

The majority of neurones studied (thirty-one units, 84 %) showed responsiveness to gentle mechanical stimulation of the skin as well as responses, of a different kind, to noxious heating of the same receptive fields. Three different kinds of responses to noxious heating of the skin have been obtained from neurones in this group.

Excitatory responses. Nineteen units (50 % of the total sample and 61 % of the units affected by noxious stimuli) responded with an increase in their rate of firing when skin temperature was increased above 40–45° C (Fig. 3*A*). Neurones of this class were considered to be excited by skin nociceptors (E-cells). They responded in a consistent way to repeated noxious stimuli, but the time course of their responses varied according to the type of preparation, i.e. spinal, intact cord, etc. Fig. 4*A* and *B* shows continuous records of the mean frequency of discharge of one E-cell in both the anaesthetized (Fig. 4*A*) and spinalized (Fig. 4*B*) states of the cat. This neurone responded to hair movement, noxious pinching and noxious heating in both states. Noxious heating in the anaesthetized

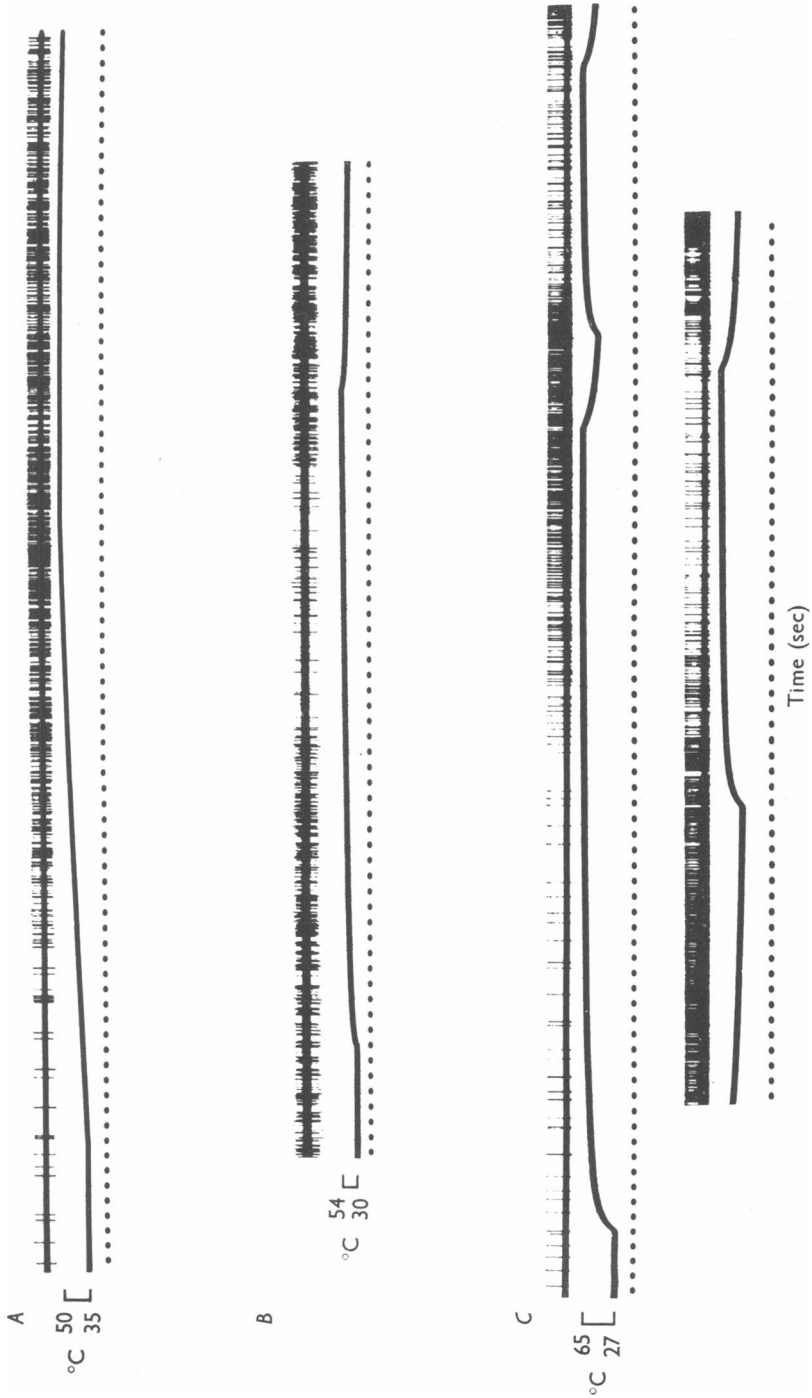

Fig. 3. Responses of three spinocervical tract neurones to heating their receptive fields. *A*, excitatory response. *B*, inhibitory response. *C*, mixed (reversed) response.

state produced a transient increase in the rate of firing that did not follow the time course of changes in superficial skin temperature (Fig. 4*A*), whereas after blocking the spinal cord at L3 the same neurone responded with increases in its rate of discharge that followed closely the time course of changes in skin temperature (Fig. 4*B*). These differences in responsivenes of spinalized and intact preparations (Fig. 5*C* and *D*) were not, however, a constant feature of the E-cells. Some showed activity which followed more closely the time course of the noxious heating in both states (Fig.

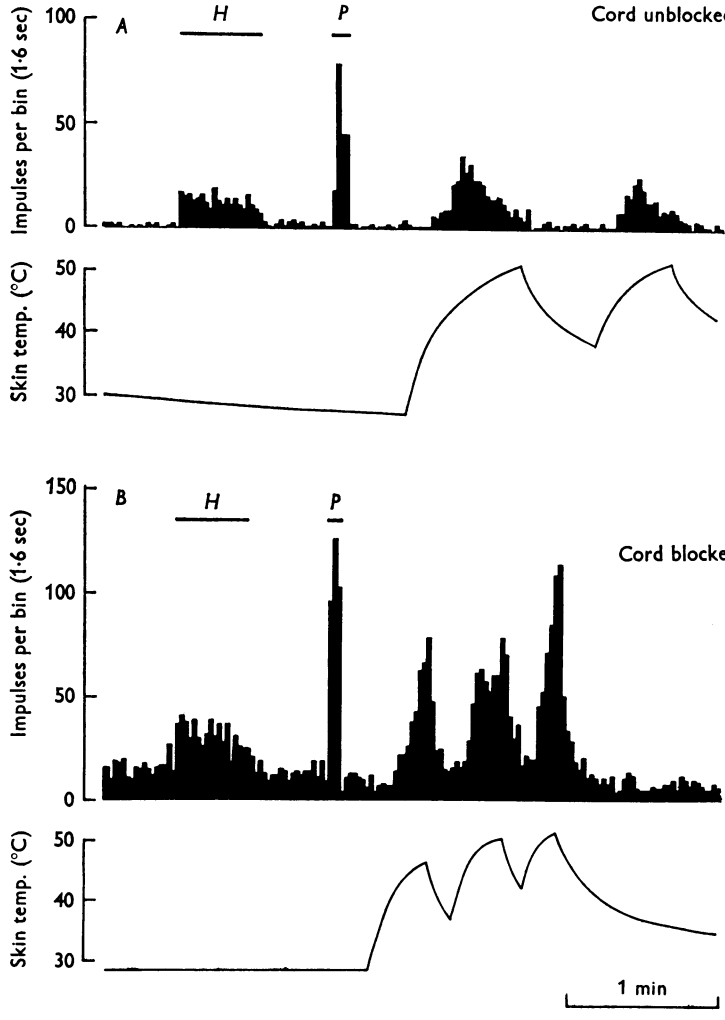

Fig. 4. Responses obtained from the same E-cell in both: *A*, the anaesthetized state of the animal; and *B*, after blocking the spinal cord. Responses to hair movement (*H*) pin-prick (*P*) and noxious heat are shown.

5*A* and *B*). Most of these that did not were recorded in decerebrated preparations.

Inhibitory responses. Six neurones (16 % of the total sample and 19 % of the units affected by noxious stimuli) were inhibited (I-cells) by heating the skin to noxious levels (Fig. 3*B*). Either spontaneous activity (as in Fig. 6*B*) or activity evoked by moving hairs within the receptive fields

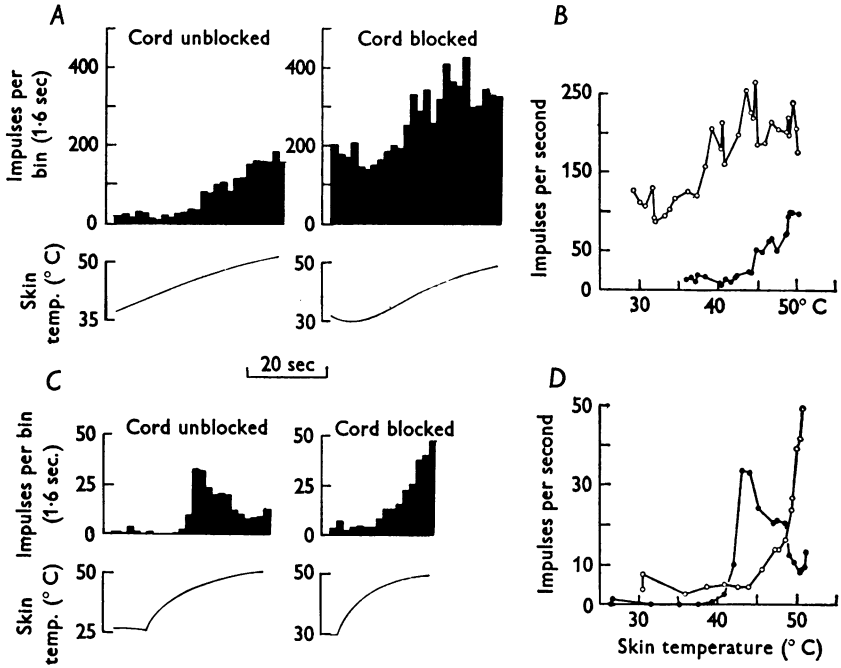

Fig. 5. Responses of two E-cells to noxious heating of their receptive fields. *A* and *B*, one unit shows the same time course to the increase in skin temperature in the intact state and after spinalization. *C* and *D*, the other unit shows a transient increase when the cord is unblocked and a continuous response after blocking the cord. Open circles in *B* and *D* = cord blocked; filled circles = cord unblocked.

of the units (as in Fig. 6*A*) were inhibited and inhibition occurred in both blocked (Fig. 6*A* upper) and unblocked (Fig. 6*A* lower) states of the spinal cord. A constant feature of these neurones was the range of skin temperatures which produced inhibition. Reduction in spontaneous or evoked activity was seen when the skin temperature reached 40–45° C but at temperatures above 55–60° C there was a return of the activity to pre-test levels (Fig. 6*C*).

Mixed responses. Six neurones (16 % of the total sample and 19 % of the units affected by noxious stimuli) showed a more complex response when noxious heating was applied repeatedly to their excitatory receptive

fields. As illustrated in Fig. 3*C* these neurones showed an increase in spontaneous activity when the skin temperature reached noxious levels but when this stimulus was discontinued activity remained at a high frequency. During subsequent noxious stimuli, which closely followed this first stimulus, a decrease in the rate of firing occurred and removal of these subsequent stimuli was accompanied by a further surge of intense activity. It seems therefore that the responses of these neurones to

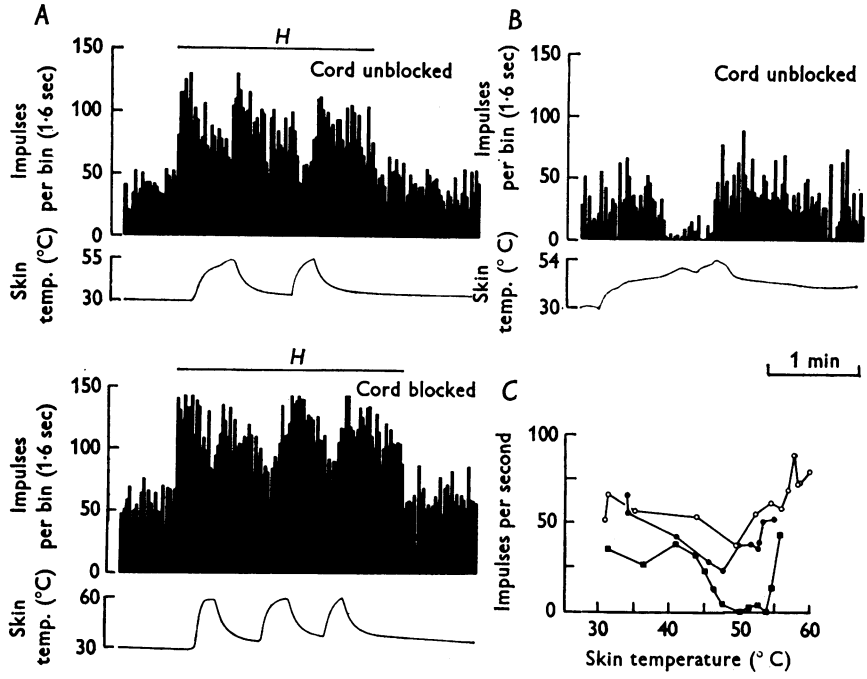

Fig. 6. Responses of two I-cells to noxious heating of their receptive fields. *A*, inhibition of activity produced by hair movement (*H*) is shown in the same spinocervical tract neurone both before (top) and after blocking the spinal cord (below). Inhibition of spontaneous activity in another unit is shown in *B*. The relationship between skin temperature and frequency of discharge is shown in *C*: open circles = spinal state with hair movement; filled circles = intact state with hair movements; filled squares = intact state with spontaneous activity.

afferent inputs from nociceptors reversed from excitation to inhibition (EI-cells). In other EI-cells this effect appeared in a different form; there was either an increase or no effect in the rate of spontaneous firing of the neurone during repeated noxious heating of the skin but increased activity after removing the heat source. This reversing type of behaviour was not affected by blocking the spinal cord. In units with the most

clearly shown reversed responses (as the one shown in Fig. 7*A*) the threshold for excitatory effects was always higher than that for inhibitory effects (Fig. 7*B*).

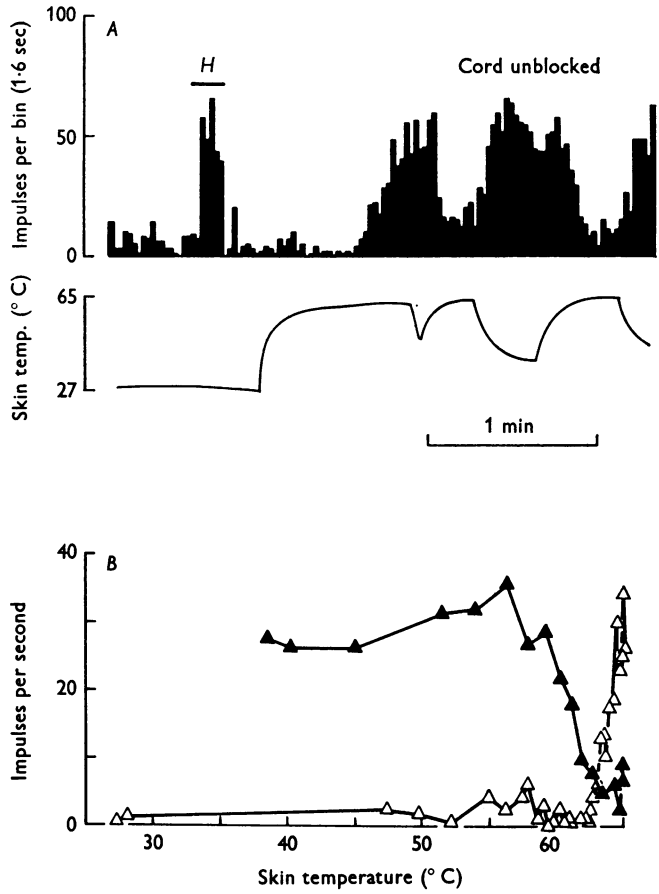

Fig. 7. Responses of one EI-cell to noxious heating of its receptive field. This unit is excited by hair movement (*H*), by the first heat stimulus and inhibited by subsequent heat stimulations. In *B* it is shown that the threshold for the excitatory response to heat (open triangles) of the unit shown in *A* is higher than the threshold for the inhibitory response (filled triangles).

The reversal or responses of the EI-cells was present and reproducible in both the spinalized and the unblocked state of the cord. This contrasts with the unique and constant inhibitory response obtained from I-cells and rules out the possibility that I-cells were in fact EI-cells reacting to a previous stimulus.

Differences between E-, I- and EI-cells

In addition to their different responses to noxious stimulation of their receptive fields some further differences between the three populations of neurones were found.

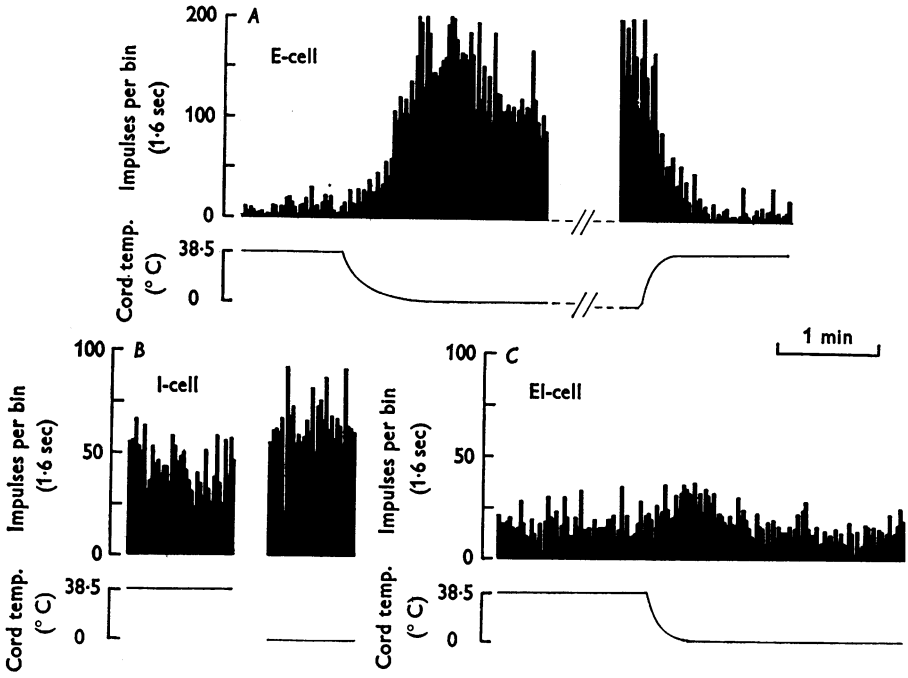

Fig. 8. Descending inhibition. The figure shows changes in the spontaneous activity of: *A*, an E-cell; *B*, an I-cell and *C*, an EI-cell; which occur when blocking the spinal cord by cooling. Note the marked increase in spontaneous activity of the E-cell, the small increase of the I-cell and the transient increase of the EI-cell.

Spontaneous activity

E-cells showed the lowest rate of spontaneous activity (0–5 Hz) in both anaesthetized and decerebrate preparations; the EI-cells were slightly higher (5–20 Hz); I-cells exhibited the highest level of background activity (30–40 Hz).

Descending inhibition

The degree of descending inhibition was assessed by cooling the spinal cord and recording changes in spontaneous activity of the spinocervical tract neurones (Fig. 8). E-cells were under the strongest descending

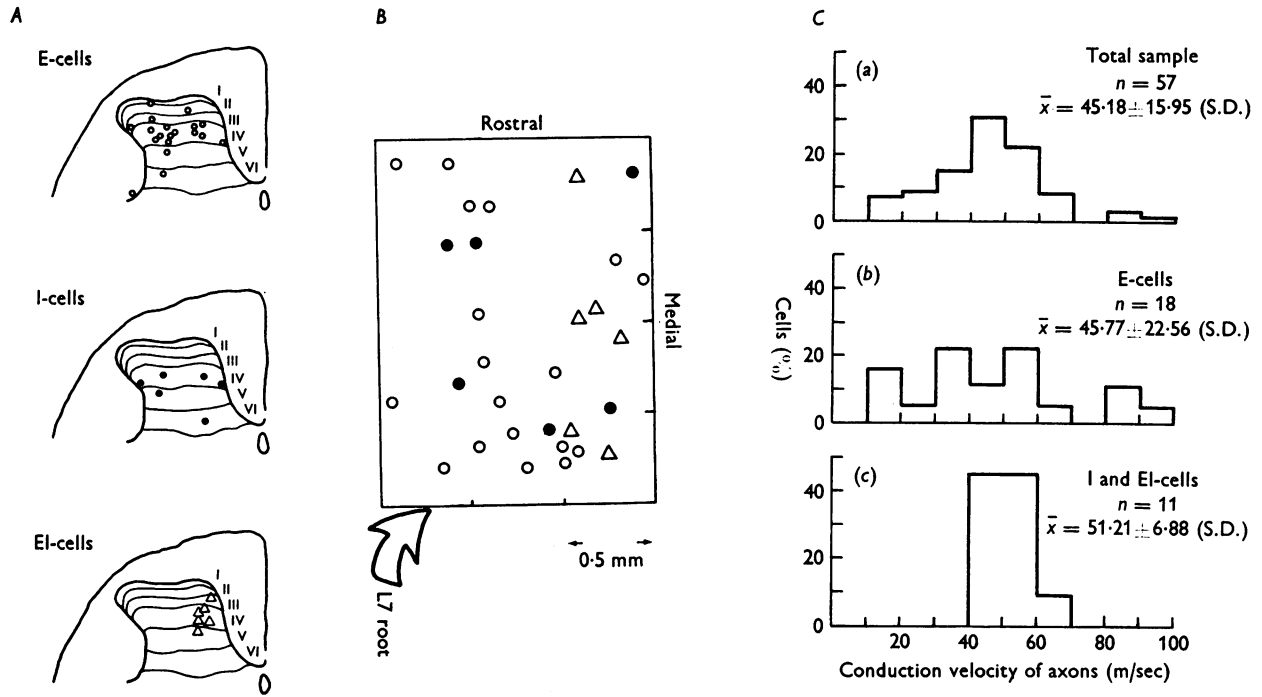

Fig. 9. Recording sites of the E, I, and EI-cells superimposed: *A*, on transverse sections and *B*, on a plan view of the left dorsal horn of the L7 and 6 segment of the spinal cord. The arrow in *B* indicates the entry point of the most rostral rootlet. *C*, histograms of the conduction velocities of spinocervical tract axons classified according to their responses to noxious stimulation: (*a*) total sample; (*b*) E-cells; (*c*) I and EI-cells. The mean and S.D. of observation are indicated.

inhibitory control, their rate of spontaneous firing being eight to twenty-times higher in the spinalized state (Fig. 8*A*). In contrast I-cells and EI-cells showed only small or transient increases in spontaneous activity, (Fig. 8*B* and *C*). Taking into account the spontaneous activity of these neurones (see above) it was seen that units with a low rate of resting discharge are subject to the most powerful descending inhibition (E-cells) whereas units with higher rates of background activity receive a less powerful descending inhibition (I and EI-cells).

Location in the dorsal horn

Fig. 9 shows the recording sites of E, I and EI-cells superimposed on transverse sections of the spinal cord (Fig. 9*A*) and on a plan view of the dorsal horn (Fig. 9*B*). The only difference was that the EI-cell recording sites were mainly in the more medial part of the dorsal horn.

Conduction velocities

The E-cells had axons with conduction velocities similar in range to that of the whole sample (Fig. 9*C*) whereas the axons of I- and EI-cells had conduction velocities within a much narrower range.

Receptive fields and non-noxious responses

No differences were found between the receptive fields of the different kinds of neurones, they were similar in both shape and size. All the three kinds of neurone were excited by moving hairs within their receptive fields. However, no attempt has been made to distinguish between different kinds of hairs and we are therefore unable to say whether particular kinds of hairs excite E-, I- or EI-cells.

Variability between cats

No differences were found in the number and kind of neurones recorded from different animals in different conditions (i.e. spinalized, anaesthetized, decerebrated).

DISCUSSION

The novel results reported in this paper establish that spinocervical tract neurones can respond in different ways to noxious stimulation of the skin. As far as the general characteristics of spinocervical tract neurones are concerned we have found no differences between our sample and those obtained in previous studies. The conduction velocities obtained are comparable with those published by Brown & Franz (1969) and Bryan *et al.* (1973) and the distribution of our recording sites in the spinal cord is coincident with that of Bryan *et al.* (1973) and with the distribution of the

extracellularly recorded spinocervical tract neurones of Brown *et al.* (1976). The location of spinocervical tract neuronal bodies, as determined by intracellular staining (Brown *et al.* 1976), is, however, restricted to a narrower region around lamina IV. This suggests that extracellular recordings pick up unit activity some distance away from the cell bodies, or that only the biggest spinocervical tract neurones are concentrated in this region. The kinds of receptive fields found in our sample of spinocervical tract neurones and their topographical representation in the spinal cord are in agreement with the somatotopic mapping of dorsal horn neurones in the lumbosacral spinal cord of the cat (Brown & Fuchs, 1975).

In contrast to the report of Brown *et al.* (1975) that 70 % of spinocervical tract neurones receive A–C fibre excitation, only 50 % of our sample showed a clear discharge when C-fibres were stimulated in the dorsal root. It is, however, known that a discharge evoked by C-fibres stimulation can be inhibited by a previous conditioning volley in the A fibres with the maximal inhibition occurring at 30–50 msec after the A discharge (Brown *et al.* 1975). We were stimulating dorsal roots and the time of arrival of the C-volley at the spinocervical tract neurones was well within this period of inhibition and it is therefore probable that some of our sample of neurones did not respond to C-fibre stimulation because of this inhibition. This is supported by the fact that some spinocervical tract neurones with no response to electrical C-fibre stimulation did, however, show an excitatory discharge in response to natural noxious stimulation of the skin when C-fibre nociceptors were presumably excited.

Particular attention has been paid in the present work to the effect of noxious cutaneous stimulation on transmission through the spinocervical tract. The kind of stimulation employed (heating) is known to excite nociceptors (Beck, Handwerker & Zimmermann, 1974) and according to behavioural experiments (Zimmermann & Handwerker, 1974) the threshold of the nocicensive escape movement in cats shows a good correlation with the thermal threshold of the population of nociceptors. We therefore assume that heating the skin surface above 40–45° C is a kind of stimulation that both excites nociceptors and evokes 'pain' reactions. The question of whether heating the skin surface to such a high level produces irreversible skin damage or alters the behaviour of other receptors is still open to discussion. In the present experiments the heat pulses were maintained for the shortest possible period and the responsiveness of the neurones to gentle mechanical stimulation of the receptive fields, before and after the noxious stimuli were applied, did not change.

Until now only excitatory responses to noxious stimuli have been reported in spinocervical tract neurones (Brown & Franz, 1969) and then only in 57 % of them. According to results from our sample, 86·5 % of

the spinocervical tract neurones were affected in one or another way by noxious stimuli. Most of the remaining 13·5 % of neurones which responded only to light mechanical stimulation were obtained in the first few experiments. In these experiments only excitatory responses to noxious stimuli were expected. When inhibitory and reversed responses were obtained a more extended set of tests was developed and very few spinocervical tract neurones were subsequently found to be unaffected by noxious stimuli. Although we cannot rule out the existence of such nociceptor-unaffected spinocervical tract neurones, we believe that the proportion of such neurones in the tract may be even smaller than 13·5 %.

Recently Iggo (1974) has proposed a new classification of dorsal horn neurones on the basis of their excitability from the skin. Three main categories of neurones can be distinguished (classes 1, 2 and 3) of which class 3 neurones are those selectively excited by nociceptors. One of the aims of this investigation was to study the proportion of class 3 neurones within the spinocervical tract. Only one neurone in our sample was of this type and only showed its receptive field in the spinalized state of the cat which points to strong descending inhibitory control of such neurones. This small proportion of class 3 neurones projecting through the spinocervical tract suggests that the spinocervical tract does not carry a major share of specific nociceptive information.

Three different kinds of responses to noxious heating of the skin have been described in this paper. Our nociceptor-excited cells (E-cells) correspond to those spinocervical tract neurones previously described by Brown & Franz (1969). We found, however, that the frequency of discharge of these neurones to noxious heat was higher than that reported by Brown & Franz (1969), being as high as 50 Hz in the anaesthetized or decerebrated preparations and 200 Hz or more in the spinalized state. These neurones receive the strongest descending inhibitory influences, show very little spontaneous activity and do not follow the time course of the noxious heat in the intact animal, whereas a marked increase in all their excitatory responses occurs after spinalization. Functionally these neurones behave as typical class 2 cells of Iggo (1974) and Handwerker *et al.* (1975). Most of our samples of E-cells from decerebrated animals did not follow the time course of the noxious heat in the unblocked state of the cord. This agrees with the recent description by Le Bars, Menetrey & Besson (1976) of an enhancement of descending inhibition of those lamina V cells responding to noxious stimuli in decerebrate cats. Of particular interest are the nociceptor-inhibited spinocervical tract neurones (I-cells) whose spontaneous activity, as well as non-noxious evoked activity, can be inhibited by skin nociceptors and that are subject to weak and phasic descending inhibition. In some way they are the counterpart of the class

3 cells of the lamina I which are selectively excited by nociceptors, show weak descending inhibition and are inhibited by sensitive mechano-receptors (Cervero *et al.* 1976*b*). The existence of I-cells in the spinocervical tract brings into question the statement that cutaneous C-fibres either excite a spinocervical tract neurone or have no other action (Brown *et al.* 1975). There appear to be two explanations. Firstly, Brown *et al.* (1975) used electrically evoked C-volleys, a technique that in synchronously exciting an unknown number of fibres from different receptive fields can produce mixed effects in the dorsal horn. The second possible explanation is that our I-cells are inhibited by nociceptors which show a clear response to heating above 40–45° C but whose axons conduct in the Aδ range (Beck *et al.* 1974). In any case the inhibitory effects reported in this paper might be produced by interactions of primary afferents by means of primary afferent depolarization. This would support one of the current hypotheses, namely that C-fibres produce primary afferent depolarization and thus cause presynaptic inhibition in A-fibres (Franz & Iggo, 1969; Jänig & Zimmermann, 1971). It is also possible that some of the inhibiting effects might be produced by decreased activity of sensitive mechanoreceptors when heated, as for example reported by Beck *et al.* (1974) for the pad slowly-adapting mechanoreceptors in the cat.

The group of cells with reversed responses to noxious heating (EI-cells) are interesting because no responses of this kind have previously been reported in dorsal horn cells and because Gordon & Manson (1967) described cells in the nucleus ventralis posterolateralis of the thalamus of the cat with similar characteristics. This nucleus receives the main output of the dorsal column nuclei. A direct projection from the spinal cord to the nucleus ventralis posterolateralis has, however, been denied in the cat (Boivie, 1971). The similarity between our EI-cells and the thalamic cells reported by Gordon & Manson (1967) leads us to postulate that an indirect pathway via the lateral cervical nucleus is responsible for the transmission of EI-responses to the nucleus ventralis posterolateralis. Further studies in the lateral cervical nucleus will be required in order to confirm such a postulate.

Recently Price & Browe (1975) have described some neurones projecting through the ipsilateral dorsolateral columns which exhibited responses to non-noxious changes in skin temperature, and concluded that they were excited by warm receptors and might possibly be spinocervical tract neurones. In contrast with these results and in agreement with Brown (1973) we have found no spinocervical tract cells which were sensitive to changes in skin temperature below 40° C. The cells reported by Price & Browe (1975) may belong to pathways other than the spinocervical tract which also project through the ipsilateral dorsolateral

funiculus but on the present evidence were unlikely to be spinocervical tract cells.

Several points of note can be made on the role of the spinocervical tract in nociception. First is the high proportion of spinocervical tract neurones that are affected in one way or another by a noxious input from the skin (more than 86% in our sample). The proportion of spinocervical tract neurones exclusively excited by nociceptors appears, however, to be extremely low and under strong descending inhibition. The majority of the cells are excited by sensitive hair follicle mechanoreceptors as well as being affected by nociceptors. Nevertheless spinocervical tract neurones are affected when noxious stimuli are applied to the skin and a possible function of these responses might be to provide signals that help in the recognition, discrimination or simply the existence and peripheral localization of potentially damaging stimuli. Information about the specified quality would need to be mediated by other pathways with a higher proportion of class 3 cells. The existence of different responses within the spinocervical tract, namely excitation, inhibition or mixed responses support this interpretation of the role of the spinocervical tract as a pathway indirectly involved in nociception, and stresses the fact that it is not possible to attribute to a single anatomical pathway a sensory-modality function.

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